



Response to: Commentary: The use of referential gestures in ravens (*Corvus corax*) in the wild

Simone Pika^{1,2*}

¹ Humboldt Research Group 'Evolution of Communication', Max Planck Institute for Ornithology, Seewiesen, Germany,

² Humboldt Research Group, Department of Linguistic and Cultural Evolution, Max Planck Institute for the Sciences of Human History, Jena, Germany

Keywords: referential gestures, *Corvus corax*, intentionality, *Pan troglodytes*, fission-fusion dynamics, cognitive tool-kit, Lyod Morgan's Canon, semantization

A commentary on

Commentary: The use of referential gestures in ravens (*Corvus corax*) in the wild

by van Rooijen, J. (2015). *Front. Ecol. Evol.* 3:113. doi: 10.3389/fevo.2015.00113

This comment fits within the longstanding ambitious agenda of inspiring interdisciplinary exchange and collaboration to bridge existing gaps between different scientific fields such as for instance Animal Cognition, Developmental Psychology and Ethology (Thorpe et al., 1972; Plooij, 1978; Raemaekers et al., 1994). Based on a recent study by Pika and Bugnyar (2011) and a response by van Rooijen (2015) it aims to emphasize the need for scientific conversations discussing definitions and methodologies used and developing a shared scientific "language" in closely related fields. Only with such a "vision" can scientific progress and development be achieved.

Furthermore, it shares the view that associating Lyod Morgan's Canon (first mentioned in Dixon, 1892) with the law of parsimony (or being animal psychology's version of Ockham's razor) has been, perhaps, the most frequent and persistent form of misrepresentation (e.g., Dewsbury, 1984; Thomas, 1998). Although originally intended to underpin a psychological approach to non-human animals rather than creating another gulf (Costall, 1998), it is curiously most often echoed "when a ray of light hits a species other than ours" (De Waal, 1999, p. 256).

Pika and Bugnyar (2011) investigated the use of two specific behaviors, SHOWING and OFFERING of objects (e.g., little stones and moss), used in natural interactions of ravens (*Corvus corax*) outside the functional domain of mating. Ravens, similar to many other corvid species but also parrots (Pepperberg, 1999), are known for their sophisticated cognitive abilities (e.g., Emery and Clayton, 2004; Bugnyar et al., 2016). The evolution of these cognitive skills may have been driven by their relatively complex social matrices with individuals spending their first years of life (~5–10 years) in non-breeder aggregations characterized by fission-fusion dynamics before they form cooperative, monogamous, territorial breeding pairs (Heinrich, 1991; Braun et al., 2012). Although Gwinner (1964), based on observations of captive individuals, already pointed out that ravens exceed other bird species in their expressive behavior and underlying flexibility, this scientific domain remained relatively unexplored in the following decades.

This is very surprising since the study of visual signals has been fascinating scientists for several centuries. The heroic ancestral figure of this research domain is Charles Darwin who wrote the first scientific treatise on the subject—*The expression of the emotions in man and animals* (Darwin, 1872). Darwin mentioned different visual signals, which were distinguished later by Green and Marler (1979) as different subcategories – "states" and "events." States include ornaments,

OPEN ACCESS

Edited by:

Christina Riehl,
Princeton University, USA

Reviewed by:

Mark Laidre,
Dartmouth College, USA

*Correspondence:

Simone Pika
spika@orn.mpg.de

Specialty section:

This article was submitted to
Social Evolution,
a section of the journal
Frontiers in Ecology and Evolution

Received: 23 August 2016

Accepted: 03 October 2016

Published: 08 November 2016

Citation:

Pika S (2016) Response to:
Commentary: The use of referential
gestures in ravens (*Corvus corax*) in
the wild. *Front. Ecol. Evol.* 4:121.
doi: 10.3389/fevo.2016.00121

coloration and any other visual signals that are permanently “on”¹, while events involve visually detected movements such as courtship displays² that are “on” for relatively short periods only. The study of visual signals also played a crucial role for many pioneer workers in the nineteenth century and inspired some of the major theories of classical ethology (e.g., Lorenz, 1939; Tinbergen, 1952; Wickler, 1965). The main foci of the early studies were on displays of events such as courtship ceremonies, feeding dances, and threat behaviors in a variety of arthropod (e.g., Drees, 1952; Crane, 1966; von Frisch, 1974), bird (e.g., Huxley, 1914; Tinbergen, 1959) and fish species (e.g., Pelkewijk and Tinbergen, 1937).

It has been argued that all of these complex movement patterns have certain aspects in common: They (a) can be characterized by a relatively high degree of rigidity, (b) are not learned from conspecifics, (c) continue to completion without further stimulation once elicited, (d) can occur spontaneously in *vacuo*, and (e) are species-specific (Thorpe, 1951; Moltz, 1965; Schleidt, 1974). The phenomenon of such a stereotypic species-specific elementary unit of behavior was first proposed by Whitman (1898) and independently discovered a couple of years later by Heinroth (1911). The main proponent of this concept however became Lorenz (e.g., Lorenz, 1932), who coined the term *Erbkoordination*. In his English publications, this term changed from first *innate behavior pattern* over *fixed motor pattern* to *fixed action pattern* (FAP, Lorenz, 1950) based on Tinbergen’s (1951) originally proposed term *fixed pattern*. During these years the emphasis on characteristics of the *fixed action pattern* transformed, with stereotypy, the “fixedness” of the act itself, becoming the main characteristic (e.g., Lorenz, 1965; Schleidt, 1974). This had several consequences: First, because of their particulate and quantitatively delineable character, FAPs became highly satisfactory analytic units for psychogenetic research (e.g., Hinde, 1956; Dilger, 1959). Second, the majority of visual events were studied as displays (*sensu* Huxley, 1914) where their adaptive function in terms of information transfer was of primary concern (Smith, 1977).

In addition, since the field of animal behavior was still mainly dominated by the theoretical paradigms of ethology and behaviorism, investigations into subsets of visual behaviors of animals such as gestures (although the term has been used but not defined by some scientists, e.g., Morris, 1958; Gwinner, 1964; Armstrong, 1965; Duncan, 1972) and postures as well as their behavioral plasticity and underlying cognitive mechanisms remained relatively unexplored.

Research on gestural abilities in relation to cognitive skills was instigated by Developmental and Comparative Psychologists interested in communicative abilities and language origins (for a recent review see Pika, 2015). By using the developmental

Piagetian and the preverbal communication perspective, they also provided operational tools to investigate whether behaviors qualify as intentional produced strategies (Piaget, 1952; Bates et al., 1979; Bruner, 1981).³

Thus in 2011, Pika and Bugnyar (2011) intrigued by the nearly-forgotten hypothesis of Gwinner (1964) applied some of these operational criteria to study whether ravens’ expressive behavior is indeed produced intentionally. They used the gesture definition developed by Pika (2008) and showed that two distinct behaviors, *SHOWING* and *OFFERING*, (i) were always directed toward a recipient (100%), (ii) were mechanically ineffective (that is, they were not designed to act as direct physical agents; 95%), and (iii) received a voluntary response (100%). Following their definition (Pika, 2008), these signals thus qualified as gestures⁴. In addition, they fulfilled certain criteria of intentionality measured by (1) adjustment to audience effects (behaviors were significantly more often directed to an attending recipient than to a non-attending recipient), and (2) response waiting [the signaler waits for a response (≥ 2 s) after the signal has been produced], providing evidence that ravens use specific communicative behaviors as flexibly produced intentional strategies (Pika and Bugnyar, 2011).

While indeed, van Rooijen (2015) lists some studies showing that other species such as dogs understand intentional referential signals produced by humans (Hare and Tomasello, 1999) and coral reef fishes may use referential gestures in inter-species interactions to solicit potential hunting partners (Vail et al., 2013), additional candidates may also be found in two additional animal taxa: Spiders and flies. For instance, spider males, similar to many other distantly related taxa, offer prey items or “wedding gifts” to respective females to increase mating success. Male *Pisaura* and *Paratrechalea* spiders however present non-nutritional “symbolic” gifts, such as seeds wrapped in silk, to respective females (Albo et al., 2011). Similarly, male dance flies (Diptera, Empididae) offer inedible wedding-presents (sometimes in the form of completely empty but impressive silk balloons) to stimulate pair formation (e.g., Kessel, 1955; Cumming, 1994).

However, the majority of possible candidates for referential gestural signaling involving inedible objects in birds (junglefowls: Kruijt, 1966, casqued hornbills: Kilham, 1956), flies (e.g., Kessel, 1955; Cumming, 1994) and spiders (Albo et al., 2011) (a) have not been tested in relation to hallmarks of intentionality, and (b) are functionally situated in the mating domain. These cases may thus only reflect the internal state of the signaler rather than also flexibly referring to an external object/event,—the hallmark of referential signaling (Evans, 1997). Nevertheless, the absence of evidence might merely reflect a paucity of data, rather than a lack of referential gestural abilities on behalf of these species. Future observational and experimental studies are thus crucially needed to verify whether referential signaling in the gestural

¹ However note that signals conveyed via coloration range on a continuum and can change relatively quickly from “states” into “events” (e.g. sexual skin of mandrills, Setchell and Dixon, 2001).

² Behavioural displays have been traditionally defined as conspicuous stereotyped movements performed in special contexts with apparent communicative functions (Shettleworth, 2009). They can provide several kinds of information concurrently (e.g., a display of a chimpanzee male combines both acoustic and visual components) and may have been shaped by natural selection to convey that specific information (Bradbury and Vehrencamp, 1998; Laidre and Johnstone, 2013).

³ Measured by criteria such as sensitivity to the social context (e.g., persistence to the goal shown by augmentations of signals until the goal has been reached, adjustment to audience effects and waiting for a response of the receiver).

⁴ However see Scott and Pika (2012) for a review of different gesture definitions and a new framework combining McNeill’s Gesture Continuum and Tinbergen’s Four “why’s” to enable the use of the term “gesture” across fields and taxa.

modality may be as rare as in the vocal domain (Evans, 1997; Price et al., 2015). If they are indeed as rare, they may have evolved in species such as for instance ravens and chimpanzees, which have to cope with highly complex and challenging social matrices. As a response, these species evolved a more flexible and diverse communicative tool-kit enabling the attribution of new meaning to signals and dissociation from behavioral domains, ends and contexts, termed semantization (Wickler, 1967).

CONCLUSION

In sum, systematic, quantitative studies are desperately needed to clarify whether intentional produced, referential gestures are more widespread in the animal kingdom than previously thought. To achieve this goal, we however need to investigate signals by using methodologies designed to (a) distinguish between the viewpoints of senders and receivers, and (b) verify whether recipients acquire information from signalers who do intend to provide it (Seyfarth and Cheney, 2003; Pika, 2012). These paradigms are crucial to bridge the apparent gulf between

the fields of Ethology, Animal Cognition and Comparative Psychology and may hopefully enable a “shared” language and a biocentric perspective onto cognitive conundrums.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and approved it for publication.

FUNDING

This work was supported by a Sofja-Kovalevskaja-Award of the Alexander von Humboldt-Foundation to SP.

ACKNOWLEDGMENTS

I am indebted to the late E. Gwinner for inspiring research on communicative skills of ravens. I thank T. Deschner, W. Wickler, and C. Boesch for constructive discussions and continuous support.

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Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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